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SEX PHEROMONES IN TWO ORBWEAVING SPIDERS, (ARANEAE, ARANEIDAE): AN EXPERIMENTAL FIELD STUDY

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ABSTRACT

Male conspecifics and congeners were attracted to screened enclosures containing female *Argiope trifasciata* and *Araneus trifolium*. Male *Argiope aurantia* were found on cages containing female *A. trifasciata* which matured earlier than wild conspecifics. Males tended to aggregate on the downwind side of cages. This evidence supports the presence of an airborne sex pheromone emitted by females of these two species of orbweavers. The use of male-attractant pheromones should produce different mating strategies than expected from random search by males. High density and clumping of females may affect reproductive success and mate competition by generating stronger signals than those of isolated females.

INTRODUCTION

Evidence of air-borne sex pheromones exists for species of several families of spiders (Araneae): Lycosidae (Tietjen 1979), Salticidae (Crane 1949), Ctenidae (Dumpert 1978), and Araneidae (Blanke 1973, 1975a, b). Crane's (1949) studies with salticids indicate that although visual cues are the primary releasers of courtship behavior, distance chemoreception also plays a role. Dumpert (1978) demonstrated increased spike frequencies in tarsal organs of male *Cupiennius salei* (Ctenidae) in response to airborne odors of living conspecific females. In a thorough review, Kaston (1936) found no conclusive evidence for distance chemoreception in lycosids. However, recent experiments by Tietjen (1979) clearly demonstrate decreased speed of locomotion by male *Schizocoza saltatrix* and *S. ocreata* in response to odors of female conspecifics. This change in speed would cause an effective increase in search intensity in the proximity of females. Blanke (1975a, b) provides clear experimental evidence of attraction of males by air-borne pheromones in *Cyrtophora cicastroa* at distances exceeding 1 m. *C. cicastroa* females began emitting pheromones on the third day after the final molt and continued secretion for 7-16 days or until copulation occurred. The study presented below provides experimental field evidence for the emission of an airborne male attractant substance by females of *Argiope trifasciata* (Forsk.) and *Araneus trifolium* (Hentz).

METHODS AND MATERIALS

I conducted field experiments testing for female sex pheromones using *Argiope trifasciata* and *Araneus trifolium* during the summer of 1980. The site was an old-field dominated by grasses, sedges, *Solidago* spp., *Rubus* spp., *Aster* spp., *Erigeron* spp., and *Fragaria* spp. It is located 8 km south of East Lansing, Michigan, USA on an experimental site of Michigan State University. I built eight enclosures covered with Lumite (Chicopee Manuf. Co.) screen on a 3 hectare portion of the larger 3-km² site. Distances between enclosures varied from 5 to 50 m, and the farthest two enclosures were less than 100 m apart. Enclosures were 4 x 6 m in area and 2 m high. I conducted two experiments with these cages, one with immatures and one with mature spiders. Beginning on 1 July 1980, I prepared each cage as follows. a 2 x 4 m patch of vegetation at either end of the cage was cut to the ground and covered with black, polyethylene plastic. Thus a 2 x 4 m patch of natural vegetation remained across the width of the center of the cage. In two cages, this vegetation was uniform and consisted almost entirely of grass. In the remaining six cages, this vegetation consisted of a 2 x 2 m patch of *Solidago* abutting a 2 x 2 m patch of grass. Cages were fumigated by covering each with plastic sheets and spraying the interior with 4 L of a Pyrethrum based insecticide. This procedure was repeated after a one week interval. The fumigation was sufficient to kill all arthropods, including most egg stages.

On 20 July 1980, I collected immature spiders of these two species from this field and nearby old-fields. I discarded all spiders appearing to be males (i. e., having swollen pedipalps). The final sample ranged from 3-7 mm total body length. Thirty *A. trifasciata* were placed in each of the two cages with solid grass patches. The six cages containing mixed vegetation received one of three different treatments. I left two empty. Two received five individuals each of *A. trifasciata* and *A. trifolium* (10 spiders per cage). The remaining two received 15 spiders of each of these species (i. e., 30 spiders per cage). One cage of each of the four pairs had its length oriented east-west, with the replicate oriented north-south. I fed spiders by hand at different rates for the following 22 days (until 15 August 1981). At this time, I removed all spiders from the cages and repeated the fumigation process twice more in each cage.

Table 1.—Numbers, species, and locations of male orbweavers on walls of indicated enclosures. Cage treatments indicate numbers and species of female spiders.

CAGE	SPECIES OF MALE ORBWEAVERS		
	<i>Argiope trifasciata</i>	<i>Araneus trifolium</i>	<i>Argiope aurantia</i>
<i>Argiope trifasciata</i> , <i>Araneus trifolium</i> : LOW DENSITY	12	4	0
<i>Argiope trifasciata</i> , <i>Araneus trifolium</i> : HIGH DENSITY	13	19	3
<i>Argiope trifasciata</i> : HIGH DENSITY	10	1	2
EMPTY	0	2	2

On 24 August 1980, I collected mature and penultimate females of the same two species in the same old-fields as before. Approximately one-third of the spiders were in the penultimate instar initially, and all of these molted to maturity by the fifth day of the experiment. Assignments of cage treatments were the same as in the experiment using immatures, except that I switched a previously empty cage with a previously low density cage. On 26 August 1980, I began the second experiment by stocking cages with spiders. Again, spiders were hand fed at different rates for 21 days, until 15 September 1980. In this experiment, both empty cages were oriented north-south, and both low-density cages east-west. Throughout both experiments, growth and maturation schedules of all females were recorded. Each day, I searched the outside walls of all cages for the presence of mature male orbweavers. Locations, numbers, and species of males, as well as local wind conditions, were recorded each day. I corroborated my observations of local wind directions using records of the Local Climatological Conditions from the National Climatic Center, NOAA.

RESULTS

On 14 August 1980, I observed seven mature male *A. aurantia* spiders on two sides of one cage at about 50 cm above the ground. The cage contained 30 *A. trifasciata*. All of the males were resting on the outside walls of the cage. Five of the spiders were on the north wall, and two on the east wall. There was a steady wind from the south-west that day, typical for southern Michigan. On the following day, five male *A. aurantia* were on this cage, but four were on the south wall and one was on the west wall. A frontal system had passed through the area on the night of 14 August and on 15 August winds were steady from the north. Males were not on any other cages these two days. Due to the details of the concurrent feeding experiment, I had fed several of these females at high rates during the entire experiment. Consequently, they had grown noticeably faster than other spiders both in experimental cages and nearby in the field. Seven of these females were in the penultimate instar on 14 August 1980, and two others were mature. Two females in the other cage containing thirty *A. trifasciata* appeared to be penultimates.

I began observations for males again on 26 August 1980, when I introduced mature and penultimate females. No males were on any cages on 26 and 27 August. Numbers, locations, and species of males on cages for 28 August through 15 September are shown in Table 1. I occasionally observed other arthropods on cage walls, including Orthoptera, Diptera, Hymenoptera, and salticid, lycosid, and agelenid spiders (both sexes). Two trends are immediately obvious from Table 1. First, only four of 75 observations of male orb weavers on cages were on the two empty cages. Second, of 26 observations of *Araneus trifolium* males on cages, 23 were on cages containing *A. trifolium* females. Of the remaining three, two were on empty cages and one was on a cage containing *A. trifasciata* only. Overlap in the presence of *A. trifasciata* and *A. aurantia* males on cages occurred only during 28 August through 31 August.

Effects of wind direction on location of males are shown in Table 2. I compared distributions of males on cage walls facing each of the four cardinal compass points for days with steady south or southwest winds versus days with north winds. Males tended to occur on walls downwind from cage interiors more frequently than would be expected at random. Differences between distributions for the two wind directions are significantly different (Chi-Square test, $P < 0.05$).

Table 2.—Comparison of numbers of males present on walls facing in each of the 4 cardinal directions on days with steady South to Southwest winds versus days with steady North winds. All species, cages, and dates and both experiments are lumped.

Wind Direction	Cage Wall				Total
	North	West	South	East	
South, South-west	13	4	4	15	36
North	1	3	6	4	14
					50

DISCUSSION

These experimental data indicate that, although males occasionally occurred on empty cages, they were attracted to cages containing female conspecifics or congeners. The fact that wind direction strongly affected distribution of males on cages and that direct contact between males and females was impossible indicate that the attractant was probably an airborne pheromone emitted by the females.

No data were available on schedules of size frequency distributions for any of these species in this area during the summer of 1980. However, previous studies indicate that mature males and females of *Argiope trifasciata* first occur in August in this area (Levi 1968, Olive 1980). *Argiope aurantia* shows a very consistent trend to be about two weeks in advance of *A. trifasciata* in developmental schedules (Tolbert 1976). *Araneus trifolium* females mature in August of the year they emerge, though some individuals apparently overwinter as matures and live through the following year. I first observed mature *A. trifolium* males in late August in previous years in this area (Olive 1980).

Although male *A. aurantia* were apparently attracted to the artificially advanced female *A. trifasciata* on 14 and 15 August, I have never observed male *A. aurantia* in the webs of female *A. trifasciata* in the field. This may be due to the fact that very few searching male *A. aurantia* survive to the dates when mature female *A. trifasciata* first become abundant. Pheromones attractive to congeners have been observed among insects, but in most cases of cross-specific attraction, species are isolated by geographic range, or time of day or season when pheromones are emitted (Shorey 1976). An alternative isolating mechanism observed in insects is that although airborne pheromones may be mutually attractive to congeners, differences in copulatory behavior or contact pheromones detected during courtship may allow males to discriminate between females of different species. However, given the double disadvantage of wasted time and energy, as well as the risk of being killed by the female, it would seem unlikely that males would depend entirely on mechanisms involving close contact. Since the two *Argiope* species overlap widely in geographic range and use of structural and vegetative habitat types (Levi 1968), habitat segregation is not a likely means of reproductive isolation. More detailed, manipulative, behavioral experiments and precise determinations of phenologies of sexes of both species might clarify this problem.

The production of pheromones by female orbweavers has interesting ramifications for several aspects of their life histories. The first involves orbweaver interactions with a major predator: hunting wasps. Mitchell and Mau (1971) and Sternlicht (1973) demonstrated the ability of parasitoids to locate insect hosts by following sex pheromone gradients. If hunting wasps were able to locate female orbweavers by means of their

pheromones, the impact of the predation on spider population would be significantly different than that expected if wasp predation was random with respect to sex and age of spiders. Conversely, this predatory tactic would exert a strong selective constraint on timing and duration of the pheromone emission period. Blanke (1975a) has observed emission periods of 17 days for *Cyrtophora cicastrorsa*. Also, the fact that pheromone emission ceases after copulation in this species is interesting. This suggests a potential conflict between selection for long periods allowing maximum mating opportunities and short periods minimizing exposure to predators. This is a fertile area for future research.

A second ramification involves the effect of spatial aggregations of females on mating success. If pheromones are the primary means of locating females, then males might be more likely to detect and locate a dense aggregation of signaling females than an isolated female. Such a phenomenon might affect the probability of male-male competition for mates (Christenson and Goist 1979) and the number of copulations available to a female. Female orbweavers were observed to aggregate in locations of high prey availability (Olive, unpublished observations). In summary, the use of male attractant pheromones should produce significantly different mating strategies and reproductive life histories than expected from random, tactile searching by males.

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